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Forty years of study on interactions between walnut tree and arbuscular mycorrhizal fungi. A review

Emma Mortier¹ · Olivier Lamotte¹ · Fabrice Martin-Laurent¹ · Ghislaine Recorbet¹

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Abstract

Walnut trees are among the most important hardwood species in the northern hemisphere, ecologically and economically. They are mainly cultivated for timber and nut production but are also attractive ornamental trees in parks. Establishing walnut orchards is difficult because seedlings have a coarse root architecture and few of them survive to transplanting. Planting success is mainly determined by the root system morphology and the nutrient status of the seedlings, so that rhizosphere conditions are critical for plant performance. Walnut trees can associate with soil-borne arbuscular mycorrhizal fungi, which are obligate biotrophs. In this association, plant-produced carbon compounds are traded against fungus-acquired soil mineral nutrients. The beneficial effect of arbuscular mycorrhizal symbiosis on hardwood seedling quality and field performance has long been known, but an integrated view is lacking about the effects of arbuscular mycorrhizas on walnut cropping. Therefore, we surveyed the literature published over the last 40 years to provide up-to-date knowledge on the relationships between arbuscular mycorrhizas and walnut trees. Our review outlines the major following points: (1) the arbuscular-mycorrhiza-mediated nutrient uptake capacity of walnut trees is associated with first- to third-order roots, and fibrous tip-ended roots are dependent on arbuscular mycorrhizal fungi, whereas pioneer roots are not; (2) early inoculation with arbuscular mycorrhizal fungi improves the survival and seedling performance attributes of transplanted walnut trees: biotization enhances walnut transplant success by increasing the number of lateral roots and plant P uptake, but these benefits are fungus- and host-dependent; (3) in the context of walnut agroforestry, deeply rooted walnut trees play a role as reservoirs of arbuscular mycorrhizal fungal propagules for the surrounding vegetation, but tree shade and soluble phosphate availability decrease walnut mycorrhizal dependency; and (4) the arbuscular mycorrhizal mycelium mediates the transport of juglone and thus plays a role in walnut tree allelopathy.

Keywords *Juglans* · Symbiosis · Rootstock · Acclimatization · Fertilization · Agroforestry · Juglone · Common mycelial networks

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1 Introduction

Walnut is the common name given to twenty-one to twenty-five species of deciduous trees belonging to the genus *Juglans* (order Fagales, family Juglandaceae), characterized by a monoecious and dichogamous habit (Manning 1978; Gleeson 1982; Germain 1992; Willis 2000; Shah et al. 2018; Bernard et al. 2018). *Juglans* trees have been classified into four sections according to leaf, flower, and fruit morphology (Table 1), namely, *Trachycaryon* (one species: *J. cinerea*), *Rhysocaryon* (black walnuts), *Cardiocaryon* (heartnuts), and *Dioscaryon* (one species: *J. regia*) (Manning 1978; Bernard et al. 2018). The genus is mostly distributed across the temperate and subtropical regions of the northern hemisphere, and several species are also found in Central America and along the Andes Mountains in western South America (Bailey and Bailey 1976; Bernard et al. 2018). By providing wood, ornamental, and nutrition value to human beings, and food and a habitat to wildlife, walnuts are among the most important trees in the northern hemisphere, ecologically and economically (Bernard et al. 2018). The fruit is renowned as a rich source of unsaturated fatty acids, proteins, vitamins E and B1, selenium, and iron (Bender and Bender 2005). It also contains a wide variety of flavonoids, phenolic acids, and related polyphenols, which have antioxidant and anti-inflammatory properties (Martinez et al. 2010; Delaviz et al. 2017; Jaiswal and Tailang 2017). Bark or leaf extracts are notably used worldwide in traditional medicine (Amaral et al. 2004). Besides nuts

and leaves, walnut is grown for its high-quality wood that is marketable for many uses, including furniture, gunstocks, veneers, and paneling (Payghamzadeh and Kazemitabar 2011). In addition to direct economic benefits, various ecosystem services among which complementarities in resource-capture strategies and enhanced soil fertility have been reported from hardwood-based agroforestry systems (Jose 2009; Bainard et al. 2011; Shukla et al. 2012).

As listed in Table 1, among the major species grown for commercial use are the Persian or English walnut (*J. regia* L.), the eastern black walnut (*J. nigra* L.), the northern California black walnut (*J. hindsii* Jeps.), and white walnut (*J. cinerea* L.). All species produce nuts, but *J. regia* is the main species widely cultivated for nut production, with worldwide in-shell walnut production exceeding 3400 kt per year (www.nutfruit.org 2014; Bernard et al. 2018). The eastern black walnut (*J. nigra* L.) is also grown for its edible nuts, but is valued economically for its high-quality wood. The nut of the black walnut is of high flavor, but due to its hard shell and poor hulling characteristics, it is not grown for commercial production (Verma 2014). Other walnut species used for valuable timber production include *J. regia*, *J. cinerea*, *J. major*, *J. neotropica*, *J. olanchana*, and *J. mandshurica* (Table 1). The primary commercial importance of the Northern California black walnut (*J. hindsii*) is as a rootstock for commercial Persian walnut (*J. regia*) orchards or as a parent of the widely used hybrid rootstock “Paradox” (*J. hindsii* x *J. regia*) (Verma 2014). Walnuts are now distributed across 60

Table 1 Main walnut species grown for commercial use according to Manning (1978), Bernard et al. (2018), and Shah et al. (2018)

Section	Species (vernacular name)	Geographic distribution	Commercial use
<i>Dioscaryon</i> (Common walnut)	<i>J. regia</i> L. (Persian or English walnut)	SE Europe, Iran to the Himalayas, China	Nuts–High-quality timber
<i>Rhysocaryon</i> (Black walnut)	<i>J. nigra</i> L. (Eastern black walnut)	Eastern United States	Timber–ornamental tree–rootstock–cosmetics–abrasive and filtering properties
	<i>J. hindsii</i> Jeps. (Northern California black walnut)	Northern California	Rootstock orchard of <i>J. regia</i> –ornamental tree–timber
	<i>J. microcarpa</i> Berl. (Texas or little black walnut)	SW United States NW Mexico	Interbreeding with <i>J. major</i> and <i>J. nigra</i>
	<i>J. major</i> Heller (Arizona black walnut)	SW United States NW Mexico	Carpentry wood
	<i>J. neotropica</i> Diels (Andean, Ecuadorian or Columbian walnut)	NW South America	Wood (floor and decoration)
	<i>J. olanchana</i> Standl. & Williams (Cedro Negro)	Guatemala	Wood (furniture and lute-making)
<i>Trachycaryon</i> (White walnut)	<i>J. cinerea</i> L. (Butternut)	Eastern United States	Lumber industry (furniture) - Medicine (cathartic properties)
<i>Cardiocaryon</i> (Heartnut)	<i>J. mandshurica</i> Maxim. (Manchurian walnut)	Manchuria, NE China, Korea	Timber–ornamental tree
	<i>J. ailantifolia</i> Carr. (Japanese walnut)	Japan	Dye

Abbreviations: SE southeastern, SW southwestern, NE northeastern, NW northwestern

countries around the globe as both commercial and ornamental trees (Avanzato et al. 2014).

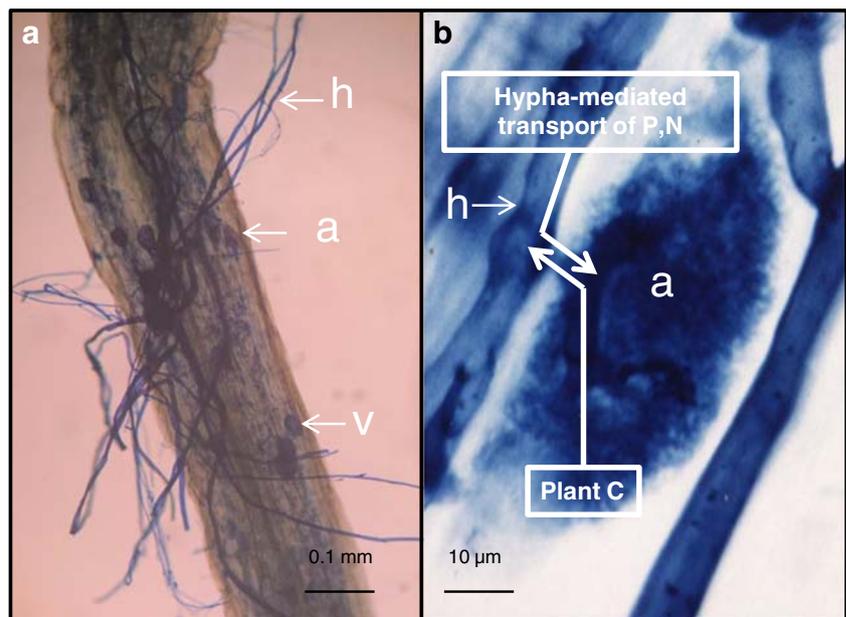
Walnut cropping mainly relies on the propagation of cultivars of biological and economic interest. To ensure top-quality orchard trees, walnuts are mainly managed and grown to a suitable size in nurseries after grafting onto seedling rootstocks selected to provide the best anchorage, vigor, and resistance or tolerance to soil-borne pests and diseases (Lopez 2004; Verma 2014). However, poor survival after planting and slow growth rates are common difficulties encountered when establishing *Juglans* orchards (Jaynes 1979; Peixe et al. 2015). Studies on hardwood species indicate that the root system morphology is one of the major determinants of seedling field performance because it provides anchorage into the soil matrix and favors nutrient uptake (Kormanik 1986; Kormanik 1989; Schultz and Thompson 1990; Grossnickle and MacDonald 2018). The nutritional status of nursery seedlings has a direct effect on factors related to their survival after planting. Storage of mineral nutrients such as nitrogen (N), phosphorus (P), and potassium (K) by seedlings has a particularly positive impact on their survival and development after planting (Landis 1985; Landis et al. 1989). In this context, the rhizosphere, namely, the region of the soil in intimate interaction with the roots, is critical for plant performance as it contains a complex array of plant-associated communities of organisms vital for soil and plant health (Bowen and Rovira 1999; Buée et al. 2009). As such, ecosystem functions can be improved by managing the rhizosphere microbiome (Bender et al. 2016).

The roots of most tree species are notably colonized by specialized soil-borne fungi that form symbiotic associations called mycorrhizas (Brundrett 1991, 2009; Kariman et al.

2018). Mycorrhizal fungi play a key role in assisting plants in the acquisition of mineral nutrients, especially N, P, and K (Smith and Read 2008; Koide et al. 2014; Garcia and Zimmermann 2014). Mycorrhizal fungi also confer protection against pathogens and root herbivores (Arya et al. 2010) and mediate carbon (C) transfer among plants (Simard et al. 1997; Lerat et al. 2002; Teste et al. 2009). *Juglans* hardwood species associate almost exclusively with arbuscular mycorrhizal (AM) fungi (Brundrett 1991, 2002; Comas and Eissenstat 2009; Comas et al. 2014), which belong to an ancient lineage of obligate biotrophs in the sub-phylum Glomeromycotina (Spatafora et al. 2016). AM fungi colonize plant roots to obtain plant-derived carbon in the form of sugars and lipids to sustain their growth and reproduction (Keymer et al., 2017). In return, AM fungi provide soil mineral nutrients to the host, which are acquired through the fungal extra-radical mycelium (ERM) that reaches soil volumes inaccessible to plant roots (Friese and Allen, 1991; Gutjahr and Parniske 2013; Rich et al. 2017; Roth and Paszkowski 2017; Wang et al. 2017). Fine (1–5 μm) fungal hyphae (Bago et al. 1998) give plants access to soil inorganic phosphate (Pi) and inorganic N in the form of nitrates (NO_3^-) and ammonium (NH_4^+) (Harrison et al. 2002; Hodge and Fitter 2010; Bücking and Kafle 2015; Chen et al. 2018). During mycorrhizal nutrient uptake, soil Pi and N are acquired by high-affinity transporters located in the extra-radical hyphae and translocated to fungal arbuscules (Fig. 1). These tree-shaped invaginations develop in root cortex cells and enable nutrient exchanges between the two partners (Gutjahr and Parniske 2013; Bücking and Kafle 2015).

AM fungi act as a major biotic component of the rhizosphere because they improve plant development and nutritional status, reduce planting stress, and increase the field

Fig. 1 Illustrations after Trypan blue staining of **a** AM fungal development in walnut roots with fungal hyphae (h), vesicles (v), and arbuscules (a), and **b** an arbuscule consisting of highly-branched fungal hyphae that develop in root cortex cells where nutrient exchanges occur between the host and the fungus



survival rate of seedlings (Carpio et al. 2003; Davies 2008). The role of AM symbiosis in improving hardwood seedling quality and field performance has long been known (Kormanik et al. 1982; Kormanik 1985; Cordell et al. 1987), but an integrated view of the agronomic role of arbuscular mycorrhizas in walnut cropping is still lacking. Based on a survey of the literature published over the last 40 years, the present manuscript aims at providing up-to-date knowledge on arbuscular mycorrhiza–walnut tree relationships. As schematized in Fig. 2, this review describes the AM colonization process of walnut as related to root morphology and anatomy. It further addresses benefits from AM biotization, which are fungus- and host-dependent. Finally, it highlights positive and negative feedbacks between walnut planting and AM fungi. The conclusion proposes future lines of research to bridge current knowledge gaps.

2 Arbuscular mycorrhizal colonization of walnut is related to root architecture and anatomy

Trees usually form two main types of mycorrhizal associations: AM associations with fungi from the phylum

Mucoromycota (Bonfante and Venice 2020), and ectomycorrhizal (EM) associations with fungi mostly from the Ascomycota and Basidiomycota phyla (Wang and Qiu 2006; Brundrett 2009). Trees within a given genus usually have the same type of mycorrhiza, and these relationships are generally also consistent within families. Juglandaceae is an outlier family in which *Carya* spp. forms the EM type, whereas *Juglans* spp. predominantly displays the AM type (Brundrett 1991). The mycorrhizal association type is not systematically related to the phylogenetic relatedness of the host tree: trees associated with different mycorrhizal types profoundly differ in root traits related to nutrient foraging (Liese et al. 2017; Kong et al. 2019). Knowledge about the root architectural and morphological features associated with AM colonization is therefore required to understand walnut acquisition of belowground resources.

2.1 Root diameter and branching order of absorptive roots

Enhanced nutrient uptake is the major benefit for AM plants. Mycorrhizal dependency has thus been defined as the plant's inability to grow in the absence of mycorrhizas at a given soil fertility level (Gerdemann 1975; Siqueira and Saggin-Júnior

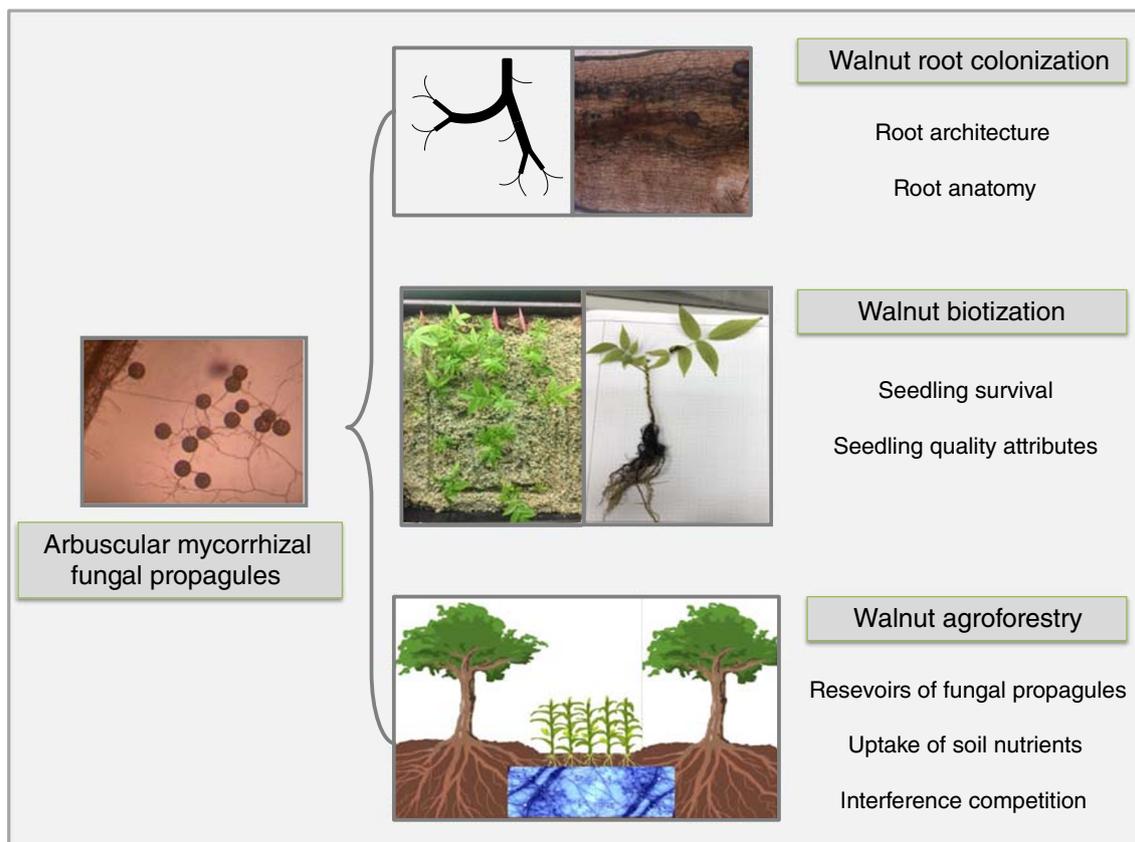


Fig. 2 Walnut tree roots interacting with arbuscular mycorrhizal fungi

2001; Janos 2007). As such, mycorrhizal dependency is an intrinsic property of a plant species or genotype, and largely controlled by the root system architecture (Baylis 1975; Plenchette et al. 1983; Janos 2007). Traits of absorptive roots (roots less than 1 or 2 mm in diameter) are indicators of the nutrient and water uptake capacities (Pregitzer 2002; Pregitzer et al. 2002; Guo et al. 2008). Plant species with thin absorptive roots are efficient in nutrient foraging and do not invest in AM fungi in P-limited soils (Bates and Lynch 2001; Hodge 2004; Liu et al. 2015). On the contrary, thick-root species have a limited intrinsic ability to absorb nutrients (Bates and Lynch, 2001). They are thus assumed to benefit from the presence of finely structured AM fungal hyphae that increase the surface area available for absorbing nutrients, especially P (Raven and Edwards 2001; Comas et al. 2014; Eissenstat et al. 2015; Liu et al. 2019). Walnut absorptive roots have a coarse root architecture. Chen et al. (2016) reported contrasted root thicknesses for *Juglans nigra* (AM-type) and *Carya glabra* (EM-type), with mean root diameters of 0.36 mm and 0.19 mm, respectively. Thicker *Juglans* spp. absorptive roots are thus able to support more arbuscular mycorrhizas *per* unit root length or mass because AM fungi form associations within cortical cells along the root axis (Brundrett 2002, 2009; Guo et al. 2008; Zadworny and Eissenstat 2011; Unger et al. 2017). In contrast, in EM associations, fungi predominantly form Hartig nets in the intercellular spaces of root tips, so that fine root systems are more adapted to EM fungal colonization (Brundrett 2002; Comas et al. 2014).

It has become increasingly clear in the last two decades that the terminal branched root system of perennial plants consists of individual units, with distinct traits (Guo et al. 2008; Salahuddin et al. 2018). Terminal root units consist of several orders that have been classified according to their branching position, with the thinnest, most distal ones termed 1st-order roots, as schematized in Fig. 3a–b (Pregitzer et al. 2002). The analysis of 23 temperate tree species, including *Juglans* spp., clearly showed that different branching orders display marked differences in anatomy (Guo et al. 2008). Based on (1) the stele-to-root-diameter ratio, (2) mycorrhizal colonization, and (3) the presence of secondary xylem (SX) and a continuous cork layer (CCL), five branching orders have been separated into two groups. In the Chinese key timber species *J. mandshurica* (Table 2), the two or three distal orders have been linked to resource uptake, as inferred from the presence of mycorrhizal colonization, a low stele-to-root-diameter ratio, and no sign of secondary growth. Fourth- and higher-order roots have no mycorrhizal colonization and display a high stele-to-root-diameter ratio, indicating a limiting nutrient uptake capacity (Guo et al. 2008). As illustrated for *J. regia* in Fig. 3c–d, these results show that AM colonization occurs in first- to third-order roots and is generally absent in the fourth and fifth orders. In summary, root anatomy and function change with position in a branching hierarchy and the AM nutrient uptake capacity of walnut trees are associated with first- to third-order roots.

Fig. 3 Illustrations of **a** root branch classification into orders numbered from 1 to 4, according to their position, with the thinnest, most distal roots identified as the first order; **b** root branch order labeling of 2-month-old *J. regia* seedlings; Trypan blue-stained extra-radical hyphae (h) of *Rhizophagus irregularis* DAOM 197198 in the vicinity of **c** first-, or **d** second- and third-order roots of 2-month-old *J. regia* seedlings

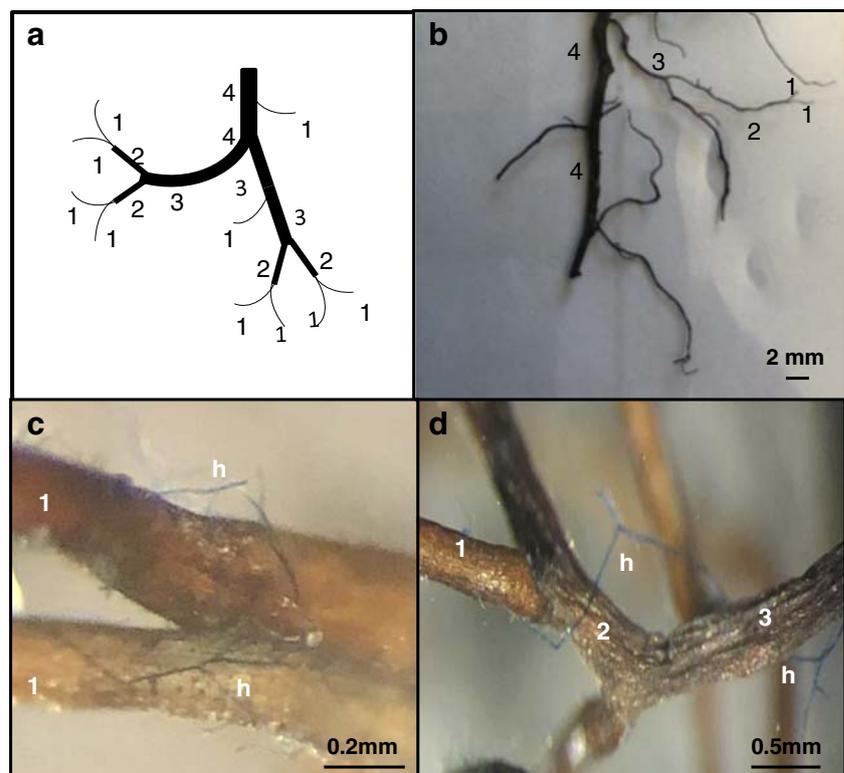


Table 2 Arbuscular mycorrhizal (AM) colonization of *Juglans* spp. as related to root traits according to [1] Guo et al. (2008) and [2] Zadworny and Eissenstat (2011)

<i>Juglans</i> species	Parameter						Ref.
<i>J. mandshurica</i> (50 years old)	Root order	1	2	3	4	5	Guo et al. (2008)
	AM colonization	Yes	Yes	Yes	No	No	Guo et al. (2008)
	Presence rate of secondary xylem (%)	0	0	< 100	100	100	Guo et al. (2008)
	Presence rate of continuous cork layer (%)	0	0	0	100	100	Guo et al. (2008)
	Mean stele-to-root-diameter ratio	0.2a	0.3a	0.4b	0.7 ^c	0.8c	Guo et al. (2008)
<i>J. nigra</i> (< 14 days old)	Root order	1 Fibrous roots	1 Pioneer roots	NA	NA	NA	Zadworny and Eissenstat (2011)
	Mean number of hypodermal layers	1.0a	5.9a				Zadworny and Eissenstat (2011)
	Passage cells (%)	15a	0b				Zadworny and Eissenstat (2011)
	AM colonization (%)	21a	0b				Zadworny and Eissenstat (2011)
<i>J. nigra</i> (> 2 years old)	Root order	1 Fibrous roots	1 Pioneer roots				Zadworny and Eissenstat (2011)
	Mean number of hypodermal layers	1.0a	4.5a				Zadworny and Eissenstat (2011)
	Passage cells (%)	10a	0b				Zadworny and Eissenstat (2011)
	AM colonization (%)	34.5a	0b				Zadworny and Eissenstat (2011)

Letters that differ within a line indicate significant ($P < 0.05$) differences

NA not addressed

2.2 Fibrous vs. pioneer roots

Further work on AM tree species, including *J. nigra*, revealed that the roots emitted as first-order branches are not all the same (Zadworny and Eissenstat 2011). All fine roots start their life as first-order roots, but only a subset grows into higher-order roots (Pagès 2002). These pioneer roots explore the soil to expand the root system and have a relatively long mean lifetime because they undergo secondary growth (Wells and Eissenstat 2001; Zadworny and Eissenstat 2011). In contrast, fibrous roots are ephemeral, do not undergo secondary growth, and are primarily associated with nutrient absorption (Wells and Eissenstat 2001; Xia et al. 2010; Zadworny and Eissenstat 2011). In both young (< 14 day-old) and mixed-age *J. nigra* roots harvested after 2 years (Table 2), the hypodermis of fibrous roots was composed of only one layer of cells, while the hypodermis of pioneer roots was multi-layered (Table 2) (Zadworny and Eissenstat 2011). In addition, the relative frequency of passage cells (cells with no evidence of secondary wall thickening) was lower in pioneer roots than in fibrous roots (Table 2). Passage cells refer to hypodermal cells deprived of a suberin lamella; they are the only cells through which AM fungi gain access to the inner cortex (Smith and

Read 1997; Brundrett and Kendrick 1988). The abundance of passage cells *per* root explains almost all the variability in the number of AM fungi penetration points *per* root (Sharda and Koide 2008). Importantly, Zadworny and Eissenstat (2011) revealed a complete lack of AM colonization in pioneer roots when compared with fibrous roots. Mycorrhizal colonization therefore strictly differs between pioneer and fibrous roots, and fibrous roots are dependent on AM fungi for nutrient acquisition.

3 Impact of arbuscular mycorrhizal biotization on walnut survival and seedling quality attributes

Walnut saplings are produced by seed propagation or plant tissue culture. Whatever the method, survival in field conditions is low (Jacobs et al. 2005a; Hackett et al. 2010). For most mycotrophic hardwood species, including *Juglans* spp., the successful establishment of seedlings largely depends on AM association and on the ability to acquire resources rapidly after planting (Smith and Read 2008). This has led to considerable interest in evaluating the significance of inoculating

walnut saplings (biotization) with selected AM fungi to enhance their survival. It is also important for nursery managers and reforestation silviculturists to identify seedling attributes quantitatively linked to planting success and to an improved field response (Burdett 1983, 1990; Grossnickle and Folk 1993; Jacobs et al. 2005a; Haase 2008; Grossnickle and MacDonald 2018; Grossnickle et al. 2018). Seedling quality evaluation includes morphological quality based on physical attributes, and physiological quality based on metabolism. Both act as a proxy for interpreting the success of field establishment of the seedlings (Haase 2008). Therefore above- and below-ground morphological and physiological parameters can help to grade the quality of mycorrhizal walnut saplings seedlings with regard to their planting success.

3.1 Survival of walnut seedlings after ex vitro acclimatization and field transplanting

Due to the heterozygosity of walnut, the characteristics of agronomical interest of the chosen cultivar are not inherited via seed propagation (Sharma et al. 2003). Consequently, plant tissue culture plays a key role in mass propagation of high-quality walnut cultivars and rootstocks with desirable traits (Payghamzadeh and Kazemitabar 2011). However, micropropagated walnut plantlets first undergo restricted Pi nutrition that limits biomass production (Barbas et al. 1993) and further display poor survival during acclimatization to the soil environment (Hackett et al. 2010). During this period, plantlets need to adapt to greenhouse conditions with decreased humidity and low sugar availability relatively to in vitro growth conditions (Fortuna et al. 1992; Schubert and Lubraco 2000; Borkowska 2002). The leaves of micropropagated plantlets display poor cuticular wax development, a low chlorophyll content, and non-functional stomata (Rohr et al. 2003; Chandra et al. 2010). Those characteristics result in excessive transpiration rates leading to desiccation, reduced photosynthetic efficiency, and carbohydrate exhaustion before replenishment from photosynthesis. Earlier studies have highlighted a beneficial role of AM fungi during the ex vitro acclimatization (Azcón-Aguilar et al. 1992; Rai 2001), but to the best of our knowledge, it has been addressed only once for *Juglans* plantlets: Peixe et al. (2015) showed that inoculation with *Glomus* spp. did not improve ex vitro survival of *J. regia* × *J. hindsii* rootstocks. In this context, it is noteworthy that (1) AM colonization during ex vitro development only takes place in young secondary roots (Azcón-Aguilar and Barea 1997) and (2) the rooting ability of micropropagated walnut plantlets is genotype-dependent (Dolcet-Sanjuan et al. 1996). Further research is needed to assess the potential of AM fungi to improve the ex vitro acclimatization of micropropagated walnut trees as related to their rooting pattern and mycorrhizal dependency.

Field-transplanted nursery trees also present variable degrees of transplant stress, described as the disruption of physiological functions in seedlings. Transplant shock is mainly caused by low nutrient availability resulting from poor root-soil contact, low water porosity of suberized roots, and mechanical root damage (Rietveld 1989; Haase and Rose 1993; Grossnickle 2005). Nurseries and reforestation programs can greatly benefit from AM biotization for the growth and establishment of seedlings used in forestry (Cordell et al. 1987; Perry et al. 1987; Pagano and Cabello 2011; Szabó et al. 2014). Early inoculation of walnut trees with AM fungi can help them survive once transplanted (Table 3). This is especially mirrored by the calculation of the mycorrhizal response (MR) index (Plenchette et al. 1983) that represents the amount of plant gains from an AM fungal associate (Baon et al. 1993). A positive MR means that seedlings benefit from the AM symbiosis. A negative MR indicates that the costs of symbiosis for the plant exceed their benefits (Janos 2007). Table 3 notably shows that the MR of walnut in terms of survival reaches up to 53 and 75% in *J. nigra* and *J. regia*, respectively. Consequently, even though indigenous AM fungi are present in the soil, early inoculation of walnut saplings with selected AM strains protects them against transplant stress.

3.2 Walnut seedling quality attributes

Seedling quality assessment aims to quantify the morphological attributes of seedlings associated with vigorous growth and development (Wilson and Jacobs 2006). This involves a combination of several characteristics, including belowground and aboveground parameters (Jacobs et al. 2005a). As illustrated for *J. nigra* and *J. regia* (Table 3), morphological grading of walnut saplings shows that AM inoculation of walnut significantly improves root biomass, total length, and volume. The MR of walnut seedling lateral roots notably reaches 22% in *J. nigra* (Table 3). Although this is not a general trait of mycorrhizal roots (Hetrick et al. 1988), AM colonization increases the number of lateral roots in most hardwood species and enhances the resource uptake activity (Guo et al. 2008; Zadworny and Eissenstat 2011). Because rooting characteristics are not easily accessible, this has led to the identification of non-destructive measurements of aboveground parameters correlated to successful hardwood development.

The size of the root system and stem volume are an indicator of the seedling survival potential (Haase 2008). In mycorrhizal *J. nigra* (Table 3), positive MRs have been recorded for the root collar diameter of *J. nigra* (Table 3). Similar observations were done with stem biomass and height, which are usually used as a proxy of photosynthetic capacity (Haase 2008; Fajardo et al. 2014). Leaf count, area, and biomass were also significantly higher in inoculated seedlings than in the controls in *J. nigra* and in the timber species *J. venezuelensis* endemic to

Table 3 Examples of significant ($P < 0.05$) positive effects of arbuscular mycorrhizal (AM) fungal inoculation on the survival and quality attributes of *Juglans* saplings

Parameter	AM	MR (%)	Inoculum	<i>Juglans</i> spp.	MPI	Number	Substrate	Reference
Survival (%)	65	53.8	<i>G. fasciculatum</i>	<i>J. nigra</i>	5	5	Fumigated soil	Kormanik et al. (1982)
	60	66.6	<i>G. mosseae</i> (BEG12)	<i>J. regia</i>	9	30	Natural nursery field	Dolcet-Sanjuan et al. (1996)
	80	75.0	<i>G. intraradiceae</i> (BEG72)		9			
Root collar diameter (mm)	6.7	11.9	<i>G. mosseae</i> and <i>G. etunicatum</i>	<i>J. nigra</i>	5	4	Fumigated soil	Schultz et al. (1981)
	7.9	27.8	<i>G. fasciculatum</i>		5	5	Fumigated soil	Kormanik et al. (1982)
	6.5	12.3	<i>G. microcarpus</i> and <i>G. fasciculatum</i>		6	3	Steam sterilized soil	Melichar et al. (1986)
Root mass (g)	8.7	19.1	<i>G. deserticola</i>		4.5	6	Fumigated soil	Dixon (1988)
	48.3	69.2	<i>G. mosseae</i> and <i>G. etunicatum</i>	<i>J. nigra</i>	5	4	Fumigated soil	Schultz et al. (1981)
	75.4	80.2	<i>G. fasciculatum</i>		5	5	Fumigated soil	Kormanik et al. (1982)
Total root length (cm)	102.0	52.9	<i>G. microcarpus</i> and <i>G. fasciculatum</i>		6	3	Steam sterilized soil	Melichar et al. (1986)
	4897	20.8	<i>G. microcarpus</i> and <i>G. fasciculatum</i>	<i>J. nigra</i>	6	3	Steam sterilized soil	Melichar et al. (1986)
	4500	33.3	<i>G. etunicatum</i>		4.5	6	Fumigated soil	Dixon (1988)
Root volume (ml)	55.6	14.4	<i>G. intraradiceae</i>	<i>J. nigra</i>	8	3	Fumigated soil	Brookshire et al. (2003)
	59.1	19.5	<i>Gigaspora. margarita</i>					
	132	22.7	<i>G. microcarpus</i> and <i>G. fasciculatum</i>	<i>J. nigra</i>	6	3	Steam sterilized soil	Melichar et al. (1986)
Number of lateral roots > 2 mm	15.5	13.5	<i>Gigaspora. margarita</i>		4.5	6	Fumigated soil	Dixon (1988)
	17.2	22.1	<i>G. deserticola</i>					
	32.1	12.1	<i>G. deserticola</i>	<i>J. nigra</i>	4.5	6	Fumigated soil	Dixon (1988)
Stem height (cm)	49.6	10.1	<i>G. etunicatum</i>		8	3	Fumigated soil	Brookshire et al. (2003)
	60.0	33.3	<i>Denticulata heterogama</i>	<i>J. venezuelensis</i>	3	10	Gamma irradiated soil	Fajardo et al. (2014)
	3.3	21.2	<i>G. mosseae</i> and <i>G. etunicatum</i>	<i>J. nigra</i>	5	4	Fumigated soil	Schultz et al. (1981)
Stem mass (g)	5.5	34.5	<i>G. microcarpus</i> and <i>G. fasciculatum</i>		6	3	Steam sterilized soil	Melichar et al. (1986)
	5.6	30.3	<i>G. deserticola</i>		4.5	6	Fumigated soil	Dixon (1988)
	6.5	13.8	<i>G. intraradiceae</i>		8	3	Fumigated soil	Brookshire et al. (2003)
Leaf area (cm ²)	1950	32.8	<i>G. microcarpus</i> and <i>G. fasciculatum</i>	<i>J. nigra</i>	6	3	Steam sterilized soil	Melichar et al. (1986)
	726	20.9	<i>G. deserticola</i>		4.5	6	Fumigated soil	Dixon (1988)
	7098	45.3	<i>Denticulata heterogama</i>	<i>J. venezuelensis</i>	3	10	Gamma irradiated soil	Fajardo et al. (2014)
Leaf count	ND	Positive	<i>G. mosseae</i> and <i>G. etunicatum</i>	<i>J. nigra</i>	5	4	Fumigated soil	Schultz et al. (1981)
	17	29.4	<i>Denticulata. heterogama</i>	<i>J. venezuelensis</i>	3	10	Gamma irradiated soil	Fajardo et al. (2014)
	ND	Positive	<i>G. mosseae</i> and <i>G. etunicatum</i>	<i>J. nigra</i>	5	4	Fumigated soil	Schultz et al. (1981)
Leaf mass (g)	4.3	100	<i>G. fasciculatum</i>		5	5	Fumigated soil	Kormanik et al. (1982)

The mycorrhizal response (MR) was calculated according to Plenchette et al. (1983) as follows: $MR = 100 \times (\text{mean value of AM plants} - \text{mean value of non-inoculated plants}) / \text{mean value of AM plants}$. *Glomus* is abbreviated G

AM mean values measured in inoculated walnut seedlings, ND non-measured parameters, MPI months post inoculation, n number of replicates per treatment

Venezuela (Table 3). Positive mycorrhizal responses recorded for walnut aboveground parameters (Table 3) have been ascribed to an increase in C assimilation by AM plants. More C is allocated to the leaves as a result of better nutrient availability to meet the growth demand (Fajardo et al. 2014). This was mirrored by increases in leaf P, N, and K concentrations of up to 35% following *J. nigra* and *J. venezuelensis* inoculation (Table 4). As illustrated in Fig. 4a—a principal component analysis (PCA) of the data reported by Dixon (1988)—(see Table 3), the developmental and nutritional values of walnut saplings are positively correlated to each other and to the mycorrhizal status of seedlings. This result holds especially true for the walnut P content and the number of lateral roots. A PCA of the results reported by Kormanik et al. (1982) (Table 3) also highlighted a positive correlation between the mycorrhizal status of walnut saplings, their survival and the total plant P content (Fig. 4b). Taken together, these results largely support that biotization with AM fungi benewalnut transplant success by increasing the number of lateral roots and plant P uptake. Multivariate analysis based on PCA also indicates that leaf area, stem height, and root collar diameter are among the non-destructive aboveground morphological parameters correlated to AM-mediated walnut field survival.

3.3 Benefits are fungus- and host-dependent

AM symbionts colonize a large number of host plant species (van der Heijden et al. 2015). Yet, the degree of root colonization by distinct AM inoculants does not correlate with the effects on the host plant. This result holds true for *Juglans* species, which do not respond in the same way to all AM fungal species (Schultz and Kormanik 1982; Dixon 1988; Fajardo et al. 2014). Total P nutrition in *J. nigra* was greater in response to colonization with a mixture of *Glomus* and *Gigaspora* species than with *Glomus fasciculatum* alone (Schultz and Kormanik 1982) (Table 5a). In *J. venezuelensis*, *Dentiscutata heterogama* outperformed *Rhizophagus manihotis* with longer roots, and higher shoot-to-root mass ratio, leaf mass ratio, leaf area ratio, and chlorophyll *a* content. Although *J. nigra* roots were unequally colonized by distinct AM fungi (Table 5b), similar symbiotic outcome in terms of leaf and stem weights (Kormanik et al. 1982), root length and the number of lateral roots (Dixon 1988) were observed. The influence of the colonization of walnut roots by AM fungi of on gene expression patterns has not yet been done (Feddermann et al. 2010), but these results support the occurrence of functional diversity among AM symbionts not reflected by root colonization parameters.

Table 4 Examples of significant ($P < 0.05$) positive effects of arbuscular mycorrhizal (AM) fungal inoculation on the mineral nutrition of *Juglans* saplings

Sapling nutrient concentration (mg / g)	AM	MR (%)	Inoculum	<i>Juglans</i> spp.	MPI	n	Substrate	Reference
Phosphorus								
Foliar	0.26	19.3	<i>Dentiscutata heterogama</i>	<i>J. venezuelensis</i>	3	10	Gamma irradiated soil	Fajardo et al. (2014)
Foliar	0.27	22.2	<i>Rhizophagus manihotis</i>					
Total	0.69	21.7	<i>Glomus fasciculatum</i>	<i>J. nigra</i>	5	5	Fumigated soil	Schultz and Kormanik (1982)
Total	0.84	35.7	<i>Glomus</i> and <i>Gigaspora</i> species					
Total	1.20	33.3	<i>Gigaspora margarita</i>	<i>J. nigra</i>	4.5	6	Fumigated soil	Dixon (1988)
Total	1.30	38.5	<i>Glomus deserticola</i>					
Nitrogen								
Foliar	7.9	35.4	<i>Rhizophagus manihotis</i>	<i>J. venezuelensis</i>	3	10	Gamma irradiated soil	Fajardo et al. (2014)
Total	2.1	23.8	<i>Gigaspora margarita</i>	<i>J. nigra</i>	4.5	6	Fumigated soil	Dixon (1988)
Total	2.1	23.5	<i>Glomus deserticola</i>					
Potassium								
Foliar	4.6	15.7	<i>Dentiscutata heterogama</i>	<i>J. venezuelensis</i>	3	10	Gamma irradiated soil	Fajardo et al. (2014)
Foliar	4.2	7.4	<i>Rhizophagus manihotis</i>					
Total	5.7	28.1	<i>Gigaspora margarita</i>	<i>J. nigra</i>	4.5	6	Fumigated soil	Dixon (1988)
Total	6.4	35.9	<i>Glomus etunicatum</i>					

The mycorrhizal response (MR) was calculated according to Plenchette et al. (1983) as follows: $MR = 100 \times (\text{mean value of AM plants} - \text{mean value of non-inoculated plants}) / \text{mean value of AM plants}$

AM mean values measured in inoculated walnut, ND non-measured parameters, MPI months post inoculation, n number of replicates per treatment

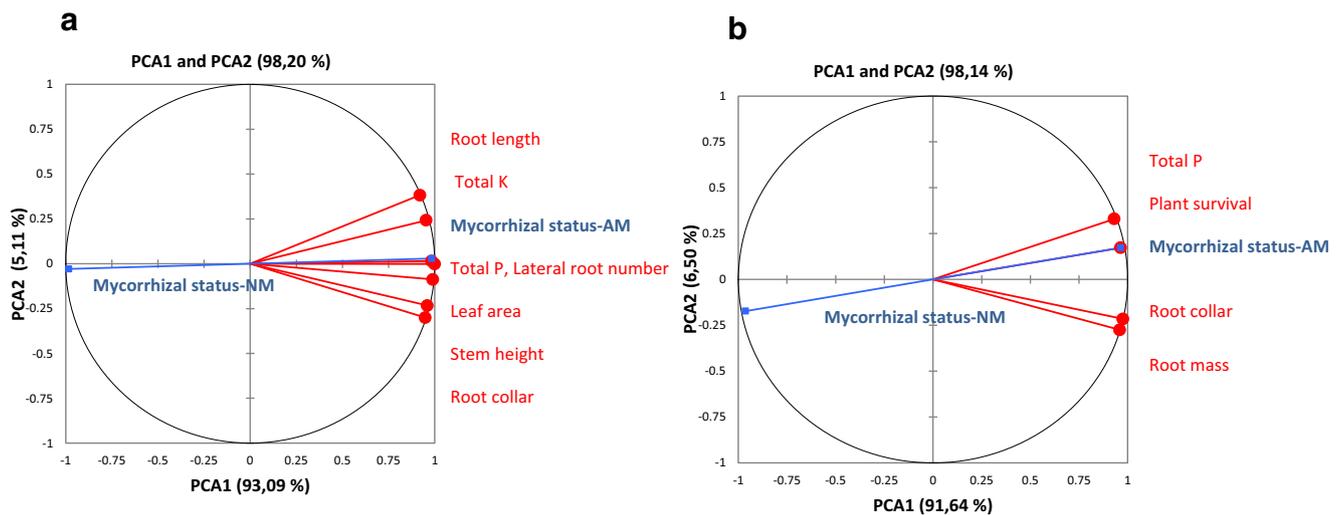


Fig. 4 Effect of mycorrhiza on walnut development and the mineral nutrient content. Growth and nutritional parameters of walnut seedlings under contrasted mycorrhizal statuses, as reported by **a** Dixon (1988) and **b** Kormanik et al. (1982), were compared by principal component

analysis, with PC1 explaining 93.09 and 91.64% of variance, respectively. AM and NM, mycorrhizal and non-mycorrhizal saplings, respectively

Besides the AM fungal isolate, the walnut cultivar also impacts seedling quality attributes and the degree of mycorrhizal colonization of *J. nigra* seedlings (Dixon 1988; Brookshire et al. 2003). Likewise, the seedling genotype/mycorrhiza interaction was significant for root collar diameter, leaf area, root weight and length, and colonization percentage, indicating a strong host-symbiont interaction effect (Dixon 1988). Therefore, walnut responses to mycorrhization vary with the nature of the fungal and plant partners, and also with soil properties (Herrera-Peraza et al. 2011). As a result, one could recommend selecting an effective mycorrhizal inoculant to improve walnut seedling quality attributes based on bioassays integrating the morphological and physiological responses of each walnut cultivar.

4 Arbuscular mycorrhizal fungi in walnut agroforestry systems

Agroforestry is a land-use practice that involves planting woody perennials with other plants in a same area, simultaneously or sequentially (Nair 1993; Garrity 2012; Waldron et al. 2017). Relatively to tree monoculture, walnut agroforestry is based on the management of plant interactions to maximize tree growth and nut/timber productivity (Dupraz et al. 1999; Mary et al. 1998; Newman 2006; Malézieux et al. 2009; Rehnus et al. 2013). Mixed cropping has been documented for several walnut species and cultivars, including the common walnut (*J. regia*), various *J. nigra* × *J. regia* cultivars, the American black walnut (*J. nigra*), and *J. mandshurica*, the Manchurian walnut (Gordon and Williams, 1991;

Mosquera-Losada et al. 2009; Mohni et al. 2009; Yang et al. 2010; Salahuddin et al. 2018). Because fine roots are key for acquiring essential nutrients and water from the soil (McCormack et al. 2015), the sustainability of mixed-species plots largely depends on belowground complementary and competitive interactions (van Noordwijk et al. 1996; Jose et al. 2006). For mycotrophic hardwood species used in agroforestry, including *Juglans* spp., soil nutrient acquisition depends on rooting traits and is also mediated by AM fungi (Janos 2007; de Kroon et al. 2012). The role of these fungi in mixed plant communities is amplified by their low host specificity, so that extra-radical hyphae connect the roots of different plant species to form a common mycelial network (CMN). CMNs linking co-cultivated plant species can mediate facilitation via nutrient transfer (Martins and Cruz 1998; Fitter et al. 1998; He et al. 2003; Leake et al. 2004; Hauggaard-Nielsen and Jensen 2005; van der Heijden and Horton 2009; Walder et al. 2012; Fellbaum et al., 2014; Gorzelak et al. 2015; Montesinos-Navarro et al. 2016), but also interference competition by releasing allelopathic chemicals that directly inhibit growth (Barto et al. 2012; Salahuddin et al. 2018). Understanding positive and negative feedbacks between mixed walnut plantations and AM fungi is therefore of critical importance in the management of mixed cropping systems.

4.1 Arbuscular mycorrhizal inoculum density and diversity in walnut agroforestry systems

To form mycorrhizas, plant roots need to come into contact with AM fungal propagules—soil-borne spores, hyphae, or

root fragments bearing fungal structures (internal hyphae or vesicles). These propagules represent the quantity of AM inoculum in the soil, i.e., the population of AM fungi (Plenchette et al. 2005). Compared with monoculture systems, the presence of trees in an agricultural system enhances AM fungal propagule abundance and diversity (Ingleby et al. 2007; Chiffot et al. 2009; de Carvalho et al. 2010; Bainard et al. 2011). Intercropping has been proposed to draw intermediate income before the plantation reaches economic maturity (van Sambeek and Garrett 2004; Mohni et al. 2009; van Sambeek 2017; Wolz and DeLucia 2019). In this case, the intercrop—winter cereals (*Triticum* spp), alfalfa (*Medicago sativa*), soybean (*Glycine max*), or summer crops (e.g., maize)—is the only income during the first 5 to 10 years; then, both trees and intercrops produce simultaneously (Mary et al. 1998; Huasen et al. 2014).

As woody perennial walnut roots allow for the year-in-year-out persistence of AM propagules, intercropping with mycotrophic species increases mycorrhiza formation in the soil and thus the abundance of AM fungi populations. A higher AM spore density was observed in wheat roots intercropped with walnut than in crop monoculture (CASDAR 2012). As previously indicated in other agroforestry systems, walnut trees act as reservoirs of AM fungi for crops or other annual vegetation (Ingleby et al. 2007; Kumar et al. 2007; Shukla et al. 2012). Walnut-wheat agroforestry plots displayed increased soil organic matter associated with a higher microbial biomass than monoculture plots (CASDAR 2012). Both the number and diversity of AM spore were enhanced in the deep horizons of walnut-wheat agroforestry fields relative to conventional monoculture (PIRAT 2012). When associated to deep walnut tree roots, AM fungi can increase the mycorrhiza-mediated uptake of soil nutrients, and thereby contribute to the nutrition of the co-cultivated species (Simard and Durall 2004; de Carvalho et al. 2010). Because mycorrhizal types differ in their physiological traits, which facilitates dissimilar soil nutrient uptake processes, the presence and diversity of fungal associations should increase resource partitioning among the different plant species with which they associate (Ferlian et al. 2018). AM fungi associated with maize and walnut roots in a same field were recently found to differ in diversity (van Tuinen et al. 2020). Concomitantly, the analysis of ^{13}C from an AM mycelium taken from the surrounding environment of intercropped walnut and maize roots indicated that part of the carbon derived from walnut trees could be transferred to maize plants (van Tuinen et al. 2020). In summary, these results underline that walnut-tree-based intercropping enhances AM fungal richness compared with monoculture systems and that AM fungi participate in the redistribution of nutrients between tree and crop roots.

4.2 Arbuscular mycorrhizal dependency in walnut agroforestry systems

As a genotypic property of plants, mycorrhizal dependency varies according to growing conditions and nutrient availability (Plenchette et al. 2005), with fine-root biomass generally lower in fertilized stands (Li et al. 2019). Compared with other deciduous angiosperms, walnut trees have great needs mainly in N, P, and K, and a relatively narrow range of soil conditions beneficial to their growth (Simorte et al. 2001; Bhattarai and Tomar 2009; Mohni et al. 2009; Gauthier and Jacobs 2011). Based on analyses of nutrient levels in healthy leaf samples and comparisons with standards recognized to be non-limiting for plant growth, nutrient deficiency in the genus *Juglans* occurs for leaf N, P, and K contents below 22, 1, and 12 g per kg of dry matter, respectively (Table 6). Fertilization enhances walnut value (Brockley 1988; Jones et al. 1995; Jacobs et al. 2005b; Salifu et al. 2006). For example, annual applications of N and P at rates of 310 kg and 620 kg per ha for 4 years significantly increased *J. nigra* nut production and leaf nutrient levels (Ponder 1998). Supplying plants with growth-limiting nutrients is one of the major factors in the control of fruit yield and quality. However, plants have long been known to respond to long-term soil inorganic P or N levels in the range of 100 mg or more per kg of soil, with inhibition of AM symbiosis development (Baylis 1967; Graham et al. 1981; Wipf et al. 2019 and references therein). As regards *Juglans* spp., a shift from 14 kg to 112 kg of both N and P per ha significantly reduced *J. nigra* root AM colonization intensity and the percentage of arbuscules (Schultz et al. 1981). In the same order of magnitude, mycorrhiza-induced growth benefits for black walnut were only reported for soil P levels below 170 kg per ha (Kormanik 1985). Assuming that the total weight of 1 ha of soil to a depth of 30 cm is approximately $3.9 \cdot 10^6$ kg (Verheye 2006), P fertility above 44 mg per kg of soil may inhibit AM colonization of walnut roots, decrease benefits of mycorrhiza, and enhance plant production costs for growers.

Besides chemical fertilization, the choice of the co-culture in walnut agroforestry has consequences on the mycorrhizal dependency of *Juglans* spp. The study of the acclimation of fine-root systems to long-term interspecific competition between larch (*Larix gmelinii*) and *J. mandshurica* trees showed that walnut displayed lower plasticity than larch as regard the branching patterns of the terminal root orders (Salahuddin et al. 2018). The arbuscular mycorrhizal colonization rates of the Manchurian walnut terminal root orders were also significantly lower (−28%) in the mixed plantation than in monoculture stands. The authors therefore proposed that the changes in mycorrhizal infection rates under interspecific competition are related to different nutrient availabilities, especially P. This hypothesis was indirectly supported by decreased specific root length and respiration rates of first-order

walnut roots when grown in mixture with larch (Salahuddin et al. 2018). Consistently, Chen et al. (2001) showed that larch roots improved the mobilization of rhizospheric rock phosphate more efficiently. This resulted in an increased available P content in the rhizosphere of *J. mandshurica* in mixed plantation relatively to monoculture. In Manchurian walnut, higher P availability in mixed plantation thus leads to a decreased investment into mycorrhizal symbionts (Salahuddin et al. 2018).

As plant-produced C is exchanged for AM fungus-acquired soil mineral nutrients, factors that negatively affect photosynthesis can reduce AM plant root colonization, soil mineral nutrient uptake, and thus plant mycorrhizal dependency (Heinemeyer et al. 2006; Gavito et al. 2019). At the tree-crop interface, light is the main limiting factor for the growth of understory vegetation in agroforestry systems, where trees reduce the availability of light to intercrops (Reynolds et al. 2007). High light intensities and long day lengths improve AM colonization and spore production in many plants (Moses et al. 2013; Konvalinková and Jansa 2016). On the contrary, tree shade, low light intensity, short day lengths, and defoliation reduce arbuscular development and spore formation because the photosynthate supply to the AM fungus decreases (Kumar et al. 2007; Shukla et al. 2009). In crop monoculture, tree shade has been evoked as the main factor responsible for the reduced AM spore density observed in agroforestry stands in spring when barley was intercropped with 30-year-old *J. nigra* and *J. regia* trees (CASDAR 2012). Overall, these studies indicate that AM mycorrhizal dependency is responsive to seasonal variation and that tree canopy management is likely to increase the development of AM fungi in walnut intercropping systems.

4.3 Arbuscular mycorrhizal fungal and interference competition in walnut agroforestry systems

Many trees of the Juglandaceae family, including *J. regia*, *J. nigra*, *J. cinerea*, *J. ailantifolia*, and *J. mandshurica*, produce juglone (5-hydroxy-1,4-naphthoquinone), an amber-colored phenolic compound poisonous to sensitive plants (Dana and Lerner 1990; Jose and Gillespie 1998; Willis 2000; Yang et al. 2010). The presence of walnut trees has a natural inhibiting effect on several species and acts as a growth-limiting factor in agroforestry systems (Strugstad and Despotovski 2012). In some typical walnut intercrops, including *Zea mays* and *Glycine max*, juglone decreases and even inhibits shoot and root growth rates, leaf photosynthesis, transpiration, respiration, and stomatal conductance. An inhibition threshold of 10^{-4} M (3 mg extractable juglone per kg of soil) was reported for maize and soybean (Hejl et al. 1993; Jose and Gillespie 1998; von Kiparski et al. 2007, and references therein). The growth of the N₂-fixing walnut companion crop black alder and autumn-olive was depressed

when hydroponically grown in solutions containing juglone at 10^{-5} M in chloroform (Rietveld 1981).

Potential juglone abundance estimated in walnut leaves, hulls, and roots ranges from less than 0.1% to 5% dry weight depending on when the samples were taken in the growing season and on the extraction techniques (Willis 2000 and citations within). Juglone gets into the soil through rhizodeposition and leaching out of decomposing leaves, hulls, fruit, or bark (Rietveld 1983; Duroux et al. 1998; Appleton et al. 2014). Juglone release affects neighboring plants up to distances ranging from 4 m (Jose and Gillespie 1998) to 27 m (Massey 1925) from the trunk of walnut trees depending on their age. Toxicity persists after tree removal for up to 1 year because juglone is persistent in the soil (Strugstad and Despotovski 2012). However, juglone could easily be degraded by polyphenol oxidase, cellulose-decomposing microorganisms or the bacterium *Pseudomonas putida* (Yang et al. 2010 and references therein). As documented in root exudates of larch intercropped with *J. mandshurica*, the increased soil microbial populations and enzyme activities in a mixed-species plantation could lead to rapid degradation of juglone (Yang et al. 2010). Consistently, Manchurian walnut trees release a large quantity of juglone into the rhizosphere, but very little juglone reaches the bulk soil (Sun et al. 2013). These results point to soil microorganisms as an important determinant of the fate and activity of allelochemicals (Inderjit 2005).

AM fungal connections transport purified or naturally released juglone (Achatz and Rillig 2014; Achatz et al. 2014). The authors found an increase in juglone transport when a mycorrhizal hyphal network was present, resulting in reduced growth of the target tomato plants. The amount of extractable soil juglone in the tomato root compartment was 271% higher when the soil was connected to the walnut leaf litter by mycorrhizal hyphae (Achatz and Rillig 2014). Because juglone is slightly hydrophobic, its movement through the AM mycelium most likely occurs via water flow along hyphae (Achatz and Rillig 2014; Achatz et al. 2014). Overall, these studies underline that AM-hypha-mediated transport of juglone contribute to the allelopathic effect of walnut in agroforestry systems, but may be modulated by the presence of rhizosphere microbial communities able to degrade juglone.

5 Conclusion

Currently available knowledge indicates that walnut trees can benefit from the development of a functional AM symbiosis. Mycorrhizal inoculation notably helps *Juglans* species to establish and improves planting performances in terms of plant survival and development. The effect of mycorrhization depends on the nature of the plant-fungus couple. As the coarse root architecture of walnut trees has a limited intrinsic ability to absorb soil nutrients, plant N and P concentrations are higher in AM-inoculated walnut seedlings than in non-mycorrhizal plants.

Table 5 Examples illustrating that the degree of colonization of walnut tree roots by distinct arbuscular mycorrhizal (AM) inoculants does not reflect host plant responses

A) Equal compatibility		Different plant responses		Inoculum	<i>Juglans</i> spp.	MPI	Substrates	References
Degree of root colonization	Intensity (%)	Plant responses	Inoculum					
Infection (%)	3.0 ^a	P concentration (mg/g)	<i>Glomus fasciculatum</i>	<i>J. nigra</i>	5	Fumigated soil	Schultz and Kormanik 1982	
84.6 ^a	2.7 ^a	0.69 ^a	<i>Glomus</i> and <i>Gigaspora</i> spp.					
71.3 ^a	Arbuscule/vesicle ratio	0.84 ^b						
Root colonization (%)	1 ^a	Total root length (m)	<i>Gi. margarita</i>	<i>J. nigra</i>	4.5	Fumigated soil	Dixon 1988	
15.5 ^a	1 ^a	3.6 ^a	<i>G. etunicatum</i>					
15.8 ^a	Mycorrhizal root length	4.5 ^b						
Root colonization (%)	6708 ^a	Total root length (m)	<i>Denticulata heterogama</i>	<i>J. venezuelensis</i>	3	Gamma irradiated soil	Fajardo et al. 2014	
44.6 ^a	9210 ^a	118 ^a	<i>Rhizophagus manihotis</i>					
43.4 ^a	6708 ^a	234 ^b						
Root colonization (%)	9210 ^a	Leaf/plant mass ratio	<i>D. heterogama</i>	<i>J. venezuelensis</i>	3	Gamma irradiated soil	Fajardo et al. 2014	
44.6 ^a	6708 ^a	31.7 ^a	<i>R. manihotis</i>					
43.4 ^a	9210 ^a	28.1 ^b						
Root colonization (%)	6708 ^a	Leaf area ratio (cm ² /g)	<i>D. heterogama</i>	<i>J. venezuelensis</i>	3	Gamma irradiated soil	Fajardo et al. 2014	
44.6 ^a	9210 ^a	80.6 ^a						
43.4 ^a	6708 ^a	68.8 ^b	<i>R. manihotis</i>					
Root colonization (%)	6708 ^a	Shoot/root mass ratio	<i>D. heterogama</i>	<i>J. venezuelensis</i>	3	Gamma irradiated soil	Fajardo et al. 2014	
44.6 ^a	9210 ^a	1.42 ^a	<i>R. manihotis</i>					
43.4 ^a	6708 ^a	1.20 ^b						
Root colonization (%)	6708 ^a	Chlorophyll <i>a</i> (µg/cm ²)	<i>D. heterogama</i>	<i>J. venezuelensis</i>	3	Gamma irradiated soil	Fajardo et al. 2014	
44.6 ^a	9210 ^a	5.9 ^a	<i>R. manihotis</i>					
43.4 ^a	6708 ^a	3.8 ^a						
Root colonization (%)	Arbuscules (%)	Similar plant responses	Inoculum	<i>Juglans</i> spp.	MPI	Substrate	Reference	
62 ^a	29 ^a	Plant responses	<i>G. fasciculatum</i>	<i>J. nigra</i>	5	Fumigated soil	Kormanik et al., 1982	
70 ^b	26 ^{ab}	Stem weight (g)	<i>G. mosseae</i> and <i>G. etunicatum</i>					
70 ^b	24 ^b	5.9 ^a	<i>Glomus</i> and <i>Gigaspora</i> spp.					
Internal hyphae (%)	Arbuscules (%)	3.3a						
62 ^a	29 ^a	7.0a						
70 ^b	26 ^{ab}	Leaf weight (g)	<i>G. fasciculatum</i>	<i>J. nigra</i>	5	Fumigated soil	Kormanik et al., 1982	
70 ^b	24 ^b	4.3 ^a	<i>G. mosseae</i> and <i>G. etunicatus</i>					
Internal hyphae (%)	Arbuscule/vesicle ratio	2.8 ^a	<i>Glomus</i> and <i>Gigaspora</i> spp.					
62 ^a	1 ^a	4.8 ^a						
70 ^b	1 ^a	Total root length (m)	<i>G. etunicatum</i>	<i>J. nigra</i>	4.5	Fumigated soil	Dixon 1988	
70 ^b	-1 ^b	4.5 ^a	<i>G. deserricola</i>					
Root colonization (%)	Arbuscule/vesicle ratio	4.5 ^a						
40 ^a	1 ^a	Lateral root count > 2 mm	<i>G. etunicatum</i>	<i>J. nigra</i>	4.5	Fumigated soil	Dixon 1988	
77 ^b	-1 ^b	15.8 ^a	<i>G. deserricola</i>					
Root colonization (%)	Arbuscule/vesicle ratio	17.2 ^a						
40 ^a	1 ^a							
77 ^b	-1 ^b							

(A) Significantly different *Juglans* spp. responses after inoculation with distinct AM fungi with equal compatibility in terms of root colonization. (B) Similar *Juglans* spp. responses after inoculation with distinct AM fungi with significant different compatibility in terms of root colonization. For each parameter, different letters indicate significant ($P < 0.05$) differences

MPI months post inoculation

Table 6 Recommended leaf contents (% dry weight) of essential mineral macronutrients for adequate growth of *Juglans* spp, updated from Blinn and Bucker (1989) and Ponder (2004). ND corresponds to not determined

	N	P	K	Ca	Mg	S	
<i>Juglans</i> spp	2.2–3.2	0.1–0.3	1.2	1.0	0.3	ND	Beutel et al. (1976)
	2.2–3.2	0.14–0.3	1.2–1.7	> 1.0	> 0.3	ND	Beede et al. (2011)
<i>J. californica</i> (California walnut)	> 2.5	> 0.11	> 1.00	ND	> 0.30	ND	Serr (1960)
<i>J. cinerea</i> (Butternut)	1.79	0.44	0.82	1.11	0.72	0.25	Gerloff et al. (1964)
<i>J. regia</i> (Persian or English walnut)	2.6–3.5	0.19–0.24	1.3–2.3	ND	0.19–0.35	ND	Kopinga and van den Burg (1995)
	2.2–2.6	0.12–0.20	1.00–1.75	0.75–20.00	0.20–0.75	ND	Smith (2003)
	2.31–2.80	0.14–0.50	1.21–2.50	1.11–2.50	0.25–0.60	0.11–0.20	Olsen (2006)
<i>J. nigra</i> (Black walnut)	1.74	0.46	1.98	3.3	0.5	0.01	McHargue and Roy (1932)
	2.0–2.6	0.10–0.25	0.75–1.30	0.50–1.10	0.15–0.45	0.05–0.25	Phares and Finn (1971)
	2.1–2.6	0.15–0.21	1.05–2.00	ND	0.21–.30	ND	Kopinga and van den Burg (1995)
	1.92	0.54	1.48	0.95	1.01	0.14	Gerloff et al. (1964)
	2.47–2.98	0.16–0.24	1.32–1.47	1.9–2.0	0.51–0.64	0.15–0.16	Mills and Jones (1996)
	2.01–5.00	0.26–0.39	2.10–4.00	0.51–1.00	0.26–2.50	0.22–0.55	Jacobs and Seifert (2004)
	2.2–3.5	0.20–0.33	0.9–2.0	1.2–2.5	0.3–0.6	ND	Reid et al. (2009)

Therefore, walnut trees benefit from symbiosis through the mycorrhizal network. However, despite the release of draft reference genomes for several *Juglans* spp. (<https://harwoodgenomics.org>; <https://treegenesdb.org>), no data is presently available on AM-specific walnut gene expression patterns. This also holds true as to the quantification of mycorrhizal symbiotic efficiency in walnut trees, i.e., C gained via the growth response to mycorrhizal colonization minus C spent to support the fungus. Fertilization was found to control the degree of AM colonization of walnut roots. This suggests that according to their nutrient status, walnut trees can stop allocating C to the symbiont when the cost of fungal maintenance exceeds the nutrient benefit. As an obvious implication in the context of walnut agricultural practices, fertilization with phosphate decreases AM colonization of walnut trees and reduces AM fungal community richness. However, in low-input agroforestry systems, deeply rooted mycorrhizal walnut trees act as reservoirs of AM fungal propagules for the surrounding vegetation. The existence of mycelial networks gathering trees and annual companion crops enhances complementarities in resource-capture strategies. While the transport of the allelochemical juglone by AM mycelial networks grown from walnut roots has been documented, no data is presently available on the role of CMNs in mediating N and P trophic plant-plant facilitation in walnut agroforestry. Finally, in the context of root-stock breeding and production, AM symbiosis may also find applications by potentially improving walnut plantlet acclimatization and adaptation to environmental conditions, including increased tolerance to various pests.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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